

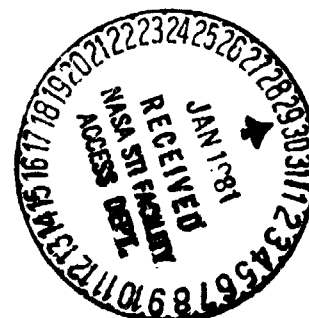
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16. Abstract Responses of primary afferents (PA) of lateral semicircular canal to sinusoidal vibration of the canal wall were studied within the range 0.05-200 Hz (mean amplitudes 5-15 microns) in immobilized frogs. Dynamic characteristics (gain, phase) relative linear velocity of the vibrator ($\mu\text{m} \times \text{s}^{-1}$) were examined. At 0.2 Hz, the gain was $5.35 \pm 3.19 \text{ imp} \times \text{s}^{-1} / \mu\text{m} \times \text{s}^{-1}$ (mean; S.D.; $n=14$) and linearly decreased if the frequency rose. Phase lag of responses relative velocity at 0.05 Hz was $49.8^\circ \pm 16.5^\circ$ ($n=13$) and at 1 Hz $97^\circ \pm 9.4^\circ$ ($n=22$). At 100 Hz phase lag was about 240° . Three groups of PA were described: wide range PA reacting in the range from 0.05 up to 60-180 Hz; high frequency PA responding in the range from 20-40 up to 100-150 Hz; low frequency PA responding in the range from 0.05 up to 2-20 Hz.			
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RESPONSES OF THE FROG PRIMARY VESTIBULAR AFFERENTS TO DIRECT VIBRATION OF THE SEMICIRCULAR CANAL

I. V. Orlov¹

In Rana temporaria frogs under the effect of curare the responses of 54 primary afferents of the lateral semicircular canal to sinusoidal vibration of its wall were studied in the frequency range of 0.05-200 Hz with an average oscillation amplitude of 5-15 mcm. The dynamic characteristics (gain and phase) of the responses relative to the linear velocity of the vibrator (scale: mcm X sec¹) were investigated. At a frequency of 0.2 Hz the gain is $5.35 \pm 3.19 \text{ imp X sec}^{-1}/\text{mcm X sec}^{-1}$, and it decreases monotonically with increase in the vibration frequency. The phase lag of the responses relative to velocity at a frequency of 0.05 Hz is $49.8 \pm 16.5^\circ$ on the average, and at frequencies on the order of 1 Hz is $97 \pm 9.4^\circ$. At a frequency of 100 Hz the lags are about 240° . Three groups of primary afferents were discovered: wide-range (81.4%), reacting in the frequency range from 0.05 to 60-180 Hz (among members of this group are those that adapt and those that do not adapt to high-frequency stimulation); high-frequency (11.1%), responding in the range from 20-40 to 100-150 Hz; and low-frequency (7.4%), for which frequencies from 0.05 to 2-20 Hz are effective. For wide-range primary afferents the time constant τ , equal to 3.7 sec, was determined. The estimated threshold amplitudes of vibration for sensitive PAs are 0.05-0.1 mcm.

Key words: semicircular canals, primary vestibular afferents, vibration, frog.

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The expediency of frequency methods of studying the function of the semicircular canals with the use of sinusoidal oscillations with corresponding levels can be explained by two reasons. One of them consists in the absence of phenomenology brought about by adaptation, acclimatization, etc., thanks to which the problems related to changes in the functional state and correspondingly to the accumulation of statistical data do not arise. In the second place, such a method makes it possible to study successfully the dynamic characteristics of the semicircular canal system, as well as of the otoliths.

The sinusoidal oscillations of vestibulometric testing units are created with the help of electromechanical gears. The frequency range of such systems normally lies in the range of 0.05-1.5 Hz [3, 8]. The breadth of this range, which is limited by the natural frequency of the testing unit, is 0.05-8 Hz only in rare cases [4]. The possibility of broadening the range is problematic. At the same time calculations [5] indicate the theoretical possibility of the semicircular canals transmitting signals having angular velocity at frequencies up to 100 Hz, and the effects observed with stimulation of the semicircular canals by high-frequency sonic and ultrasonic oscillations [12] or short mechanical impulses [1] indicate that the sensory epithelium of the canals can be excited by stimulation in a wide range of frequencies.

The goal of the present work was an investigation of the responses of the primary afferents of the lateral canal of the frog to direct vibration of its wall in the range of subsonic and low sonic frequencies. /45

Procedure

The work was conducted on Rana temporaria male frogs weighing about 40 g that had been immobilized with tubocurarine. Preparation of the left labyrinth from the bottom of the labyrinthine capsule uncovered the ampular and middle portions of the lateral semicircular canal and the branch of the 8th nerve that innervates it. The spikes in the primary afferents of the lateral semicircular canal were recorded by tungsten microelectrodes with end

diameter of about 1 mcm and impedance of 2-10 mohm at a frequency of 2 kHz, connected to the input of the noise-free discharge repeater in a KP-303G field-effect-transistor, which operates in the transistor preamplifier. The details of the procedure have been previously described [2].

For stimulation of the lateral semicircular canal an end-fused glass rod (diameter of the end 0.3 mm) was used, which was embedded in a quartz resonator (piezoelectric crystal with resonance oscillation frequency in air of about 80 Hz), the plates of which were connected to the output of the G6-14 subsonic frequency generator that was operative in the generation of sinusoidal oscillations (range of used frequencies: 0.05-200 Hz). The vibrator, embedded in the three-coordinate manipulator, made contact of the rod with the membranous wall of the middle part of the lateral semicircular canal possible. The criterion of contact of the rod and the canal wall was impact with which shifts of the endolymph in the lateral semicircular canal and consequently changes in the impulsation frequency of the afferents were not observed in the absence of sinusoidal oscillations. The direction of the movement of the glass rod comprised an angle of about 60° with the long axis of the canal. The rod's sinusoidal oscillations were monitored by the differential photodiode and amplifier of a Cl-18 oscilloscope and recorded on moving film and tape of an automatic recorder. Photorecording made it possible to measure the phase of the vibrator's oscillation relative to the generator's output tension. Measurements of the phase shifts between the electrical and mechanical sinusoids were used for the introduction of a time correction in the recording of spikes and stimuli on magnetic tape. The latter were recorded in the form of marks indicating the peak of the electrical sinusoid.

The frequency-amplitude characteristics of the vibrator were obtained on the basis of measurements of the double peak amplitude of its oscillations under a microscope with respect to the

values of the output tensions and frequencies of the generator. This made it possible to measure the maximum (peak) linear velocity of the vibrator (V_{\max} , $\text{mcm} \times \text{sec}^{-1}$) according to the formula $V_{\max} = 2\pi A/T$, where A is the amplitude of the diffraction of the piezoelectric crystal in mcm and T is the period of its oscillation in sec . In the 0.05-100 Hz frequency range the maximum velocity, with account made for the nonlinearity of the characteristics of the vibrator, altered within the range of $2.0-16.0 \times 10^4 \text{ mcm} \times \text{sec}^{-1}$.

Poststimulus histograms (PSHG) were constructed for the evaluation of the responses of the primary afferents of the lateral semicircular canal. The basis of the PSHG was synchronized with the peak of the generator's electrical sinusoid, and its total time corresponded to the period of the sinusoid. The PSHGs made it possible to study the dynamic characteristics of the primary afferents of the lateral semicircular canal--gain in velocity and phase shifts between the peak of the response and the peak of the stimulus, which causes utriculopetal displacement of the endolymph in the lateral semicircular canal.

The PSHGs were constructed on an M4030 computer². Part of the data was obtained with the help of a digital system that measured the number of spikes in a given time interval. The responses of 54 units were recorded.

Results of the Investigation

All the recorded units of the lateral semicircular canal belonged to the basic type, which is recorded on the utriculopetal deflection of the cupula by increase in the impulsation frequency [7, 11]. The utriculopetal displacement of endolymph and the similar deflection of the cupula occurred during that half period of the sinusoid when the glass rod of the vibrator put pressure on the membranous wall of the

² Program authors--S. K. Yegorov and Zh. A. Pershin (Computer center of the I. I. Pavlov Institute of Physiology of the USSR Academy of Sciences).

canal. The amplitude of the oscillations was usually 5-15 mcm from peak to peak, although the most sensitive units reacted to a variation of the vibrator equal to a value of 0.05-0.1 mcm according to calculations. Responses to vibration with different frequencies are presented in Fig. 1.

The primary afferents of the lateral semicircular canal of the frog were characterized by spontaneous activity, the frequency of which fluctuated with the range 0.5-35 imp X sec⁻¹ (average 6.5 imp X sec⁻¹, n = 20).

In accordance with the classification [8] the responses in which the lower frequency limit does not reach zero are called "all-round" ("all-round type, Fig. 1, 1-3). Along with this it was also possible to observe "cut-off" responses ("cut-off" type) in which the minimal frequency is zero (Fig. 1, 4-10). /50

Two types of response asymmetry were observed in the experiments. The first of them is related to shortening of the response time during increase of the stimulation frequency, which is noted especially well in the case of cut-off responses. With this the ratio of the duration of the unit's silence to the duration of its discharge in the 0.05-10 Hz frequency range for 10 units was 0.2-0.84 (0.52 ± 0.13 , average, standard deviation, n = 87), and it differed from the ideal case in which the cut-off unit would have discharged during the half period of stimulation and the indicated ratio would have been 1.0.

The second type of asymmetry [8] is related to the fact that the peak value of the frequency in the response does not always agree with the average period of the discharge. Therefore the response peak either is ahead of its average point, which corresponds to a positive shift, or lags behind it (negative shift). In the experiments these values fluctuated in the range from +32 to -43°. /51

The value of the gain of the primary afferents characterizes their dynamic properties in the range of used frequencies. The ratio

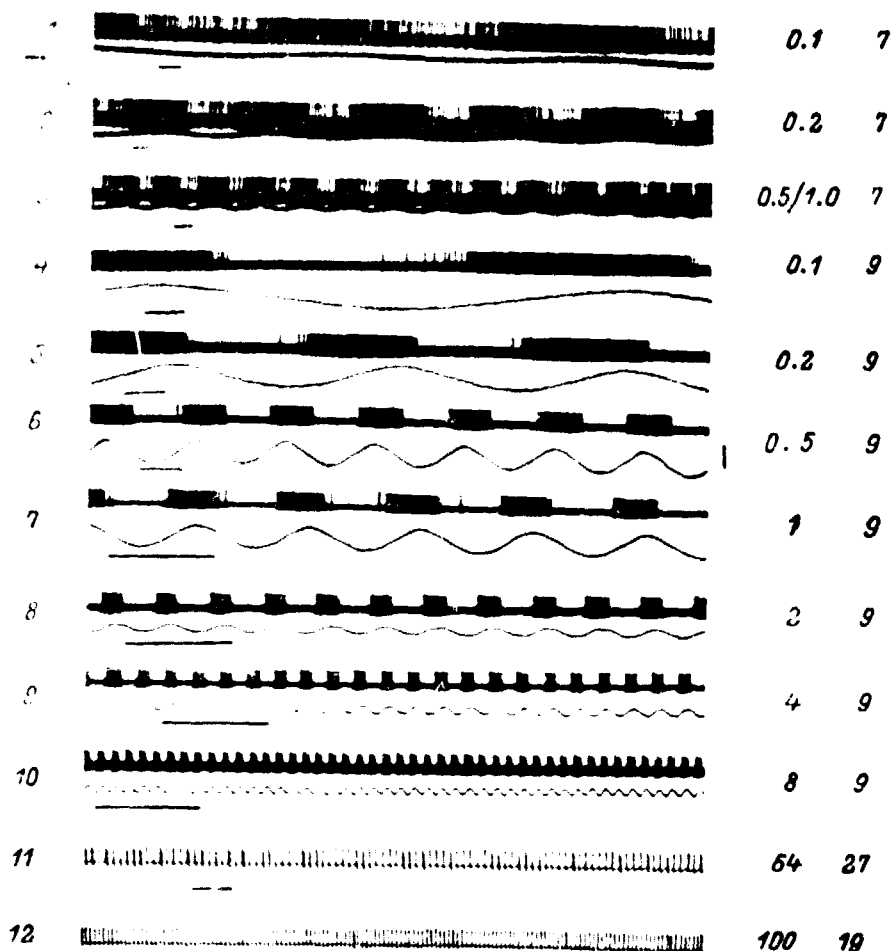


Fig. 1. Responses of afferents of the lateral semi-circular canal of the frog to sinusoidal vibration with varying frequencies.

1-3 - responses of the all-round type (unit No. 51);
4-12 - responses of the cut-off type (unit No. 47).

Upper path - nerve impulsion; lower path - coordinate of the vibrator (deviation up corresponds to the utriculopetal direction of movement). Calibration: 1 sec (1-10); 100 msec (11, 12); 1 mV. Denoted by the numbers at right: vibration frequency in Hz and its amplitude in mcm.

of the amplitude of the output signal to the amplitude of the input action is commonly called the system gain. The gain is identical to the amplitude-frequency characteristics of the system [9]. In our case gain in velocity was understood as the ratio of the peak amplitude of the response ($\text{imp} \times \text{sec}^{-1}$) to the peak velocity of the vibrator ($\text{mcm} \times \text{sec}^{-1}$). In accordance with theoretical considerations [8]

the gain in velocity (G_v) for the two indicated types of responses is calculated differently. In our case the gain for responses of the all-round type was determined from the formula $G_v = B/V_{\max}$, where B is the value of the mode of the empirical distribution, taken from the average PSHG, divided by the product of the value of the PSHG bin (in sec) by n (number of repetitions); and V_{\max} is the peak velocity of the vibrator. The value B has a dimension of $\text{imp} \times \text{sec}^{-1}$. Consequently gain in velocity in the given case has a dimension of $\text{imp} \times \text{sec}^{-1}/\text{mcm} \times \text{sec}^{-1}$. For the cut-off type responses, which are encountered more frequently in the experiments, the gain was determined according to the formula

$$G_v = \frac{B}{\max[(1 - \cos \pi(L/P))]}$$

where L is the length of the discharge (in sec) and P is the period of the stimulus (in sec) ($[B]$, modified).

The relationship of the gain in velocity to the stimulation frequency for 10 units is presented in Fig. 2. For most units the gain at frequency of 0.05 Hz was maximal and it fell with increase in frequency. The values of the gain at frequency of 0.05 Hz varied within the limits of 2.6-35.1 $\text{imp} \times \text{sec}^{-1}/\text{mcm} \times \text{sec}^{-1}$ (average 14.9 with $n = 14$). The relationship between frequency and gain (in logarithmic scale) is linear and has a proportionality coefficient approximately equal to -0.7. It should be noted that measurement of gain has significance in the frequency range where the primary afferents still give a more or less long discharge and not a separate spike in response to each period of the sinusoid. Otherwise the value of B going into the gain formula will grow only as a result of decrease in the value of the PSHG bin that goes into the denominator of the fraction and not as a result of increase of the response, which goes into its numerator. This would necessarily distort the results. Therefore it is expedient to consider the frequency 8-10 Hz as the real boundary vibration frequency in the given conditions. The relation of the average normalized gain to the vibration frequency for 22 primary afferents is shown in Fig. 2. Unit gain was taken at a frequency of 0.2 Hz, where it is equal on the average to $5.35 \pm 3.19 \text{ imp} \times \text{sec}^{-1}/\text{mcm} \times \text{sec}^{-1}$.

The phase shift ϕ (in degrees) was determined according to the

formula $\phi = (\Delta T/P) \times 360^\circ$, where ΔT is the difference in time between the velocity peaks of the vibrator and the response (in sec) and P is the period of the stimulus. The minimal phase shifts (time lag of the response peak relative to the velocity peak) were observed at a frequency of 0.05 Hz, where they were $49.8 \pm 16.5^\circ$ (average, standard deviation, $n = 13$). With increase in the stimulation frequency the phase shifts increased, reaching a value of $97.0 \pm 9.4^\circ$ ($n = 22$) at a frequency of 1 Hz. Subsequently the phase angle practically did not change during vibration to frequencies on the order of 20-30 Hz, on the exceeding of which it again increased. At frequencies of 60 and 100 Hz the phase lags grew sharply, reaching a value on the order of 240° at a frequency of 100 Hz. Phase shifts for 10 units and average normalized shifts for 22 units are presented in Fig. 3.

In terms of frequency characteristics the primary afferents can be separated into 3 groups. To the first of them, the most numerous (44/54, or 81.4%), belong wide-range units, in which the lower boundary of the frequency range lies in the range of 0.05 Hz (and, probably, lower), and the upper--in the range of 60-180 Hz. In this case part of the wide-range units did not display adaptation during 10-second stimulation (Fig. 1, 12, and also the "basic" unit in Fig. 1, 11). Other units /52 belonging to this group, on the other hand, in the given conditions could be classified as quickly adapting ("auxiliary" unit in Fig. 1, 11). No special quantitative investigations of the adaptation phenomenon during high-frequency vibration were carried out.

To the second group (6/54, or 11.1%) belonged high-frequency units in which responses to vibration appeared starting only with 20-40 Hz. With low-frequency stimulation responses were completely absent in them. The upper boundary of the frequency field for such units lies in the range of 100-150 Hz.

To the third group (4/54, or 7.4%) belonged low-frequency units that react to stimulation in the frequency range from 0.05 to 20 Hz (in one case only to 2 Hz). Responses in them are completely blocked with an insignificant increase in frequency.

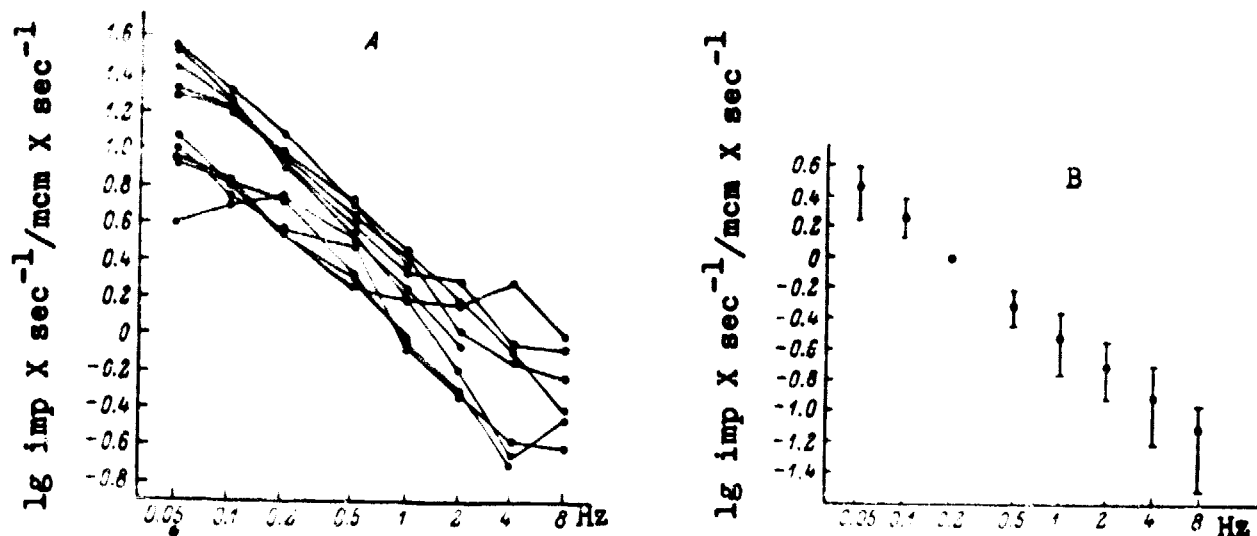


Fig. 2. Relationship of gain in velocity to vibration frequency. A - individual plottings for 10 units; B - average normalized plottings for 22 units (averages and the standard deviation are given). Gain at a frequency of 0.2 Hz is taken as a unit. Along the ordinates - gain in $\lg \text{imp} \times \text{sec}^{-1} / \text{mcm} \times \text{sec}^{-1}$; along the abscissas - vibration frequency in Hz.

Thus, for 92.5% of the units the upper boundary of the vibration frequency at which responses are still observed lies in the range of 100-150 Hz. It may be noted that the wide-range units are characterized by a larger gain in the low-frequency range than are units of the other two groups.

The number of recorded neurons, not being sufficiently representative, gives an indication of the different functional variations of the primary afferents that innervate the lateral canal of the frog.

On the basis of the responses of the primary afferents the time-setting constant τ was determined ($\tau = \Delta / \omega$ in the torsion pendulum equation for the cupuloendolymphatic system [4], where π is loss and Δ is the returning couple). This constant can be derived from the correlation $\tau = (\frac{1}{2} \pi f) \text{tg } \phi$ [4] for the case of low-frequency stimulation (0.05 Hz), where f is the stimulation frequency in Hz and ϕ is the phase shift in degrees. The value of τ in the wide-range units fluctuated within the range 1.2-9.2 sec (average: 3.7 sec, $n = 11$).

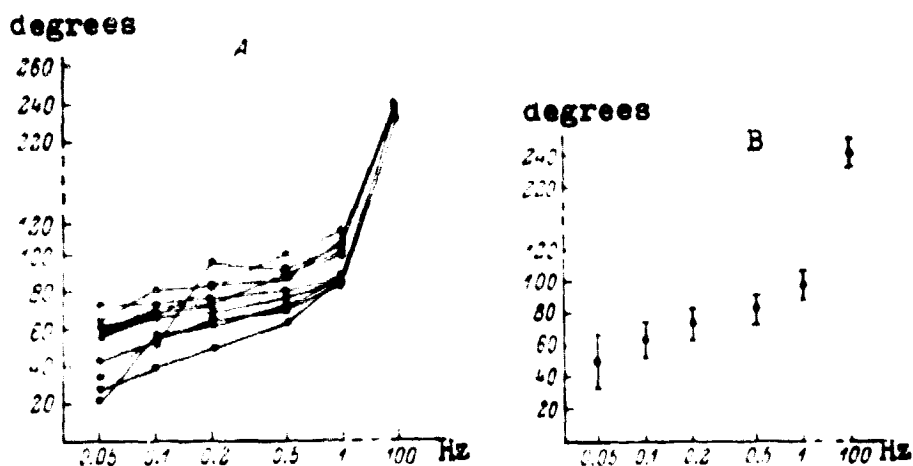


Fig. 3. Relationship of the phase shifts of the responses to the vibration frequency.

A - individual plottings for 10 units; B - average normalized plottings for 22 units. Along the ordinates - phase angles in degrees; along the abscissas - vibration frequency in Hz.

Discussion of Results

With sinusoidal vibration the primary afferents of the lateral canal display frequency-dependent dynamic characteristics--gain and phase shifts. The course of the corresponding curves is qualitatively identical to the results obtained with the use of sinusoidal oscillations of a rotating testing unit in works on mammals as well as on cold-blooded animals. In these works it has been shown that the primary afferents of the semicircular canals can react to angular acceleration, angular velocity or coordinate [3, 6, 10]. Speaking of these three physical factors, which fluctuate during the sinusoidal stimulation, it must be noted that they are interrelated by a certain relationship: the coordinate phase lags from the velocity by 90° , and from acceleration by 180° . In this work the gain and phase of the primary afferents of the semicircular canal of the frog were considered relative to the peak linear velocity of the vibrator, which in the given instance can be considered the physical analog of the angular velocity, since both these factors evoke a qualitatively identical physiological effect--displacement of endolymph in the canal. Gain in velocity in the frog at a frequency of 0.2 Hz is on the average equal to $5.35 \text{ imp} \times \text{sec}^{-1}/$

mcm X sec⁻¹. For qualitative comparison it is possible to introduce the average value of the gain in velocity for first-order vestibular neurons of the cat: 0.76 imp X sec⁻¹/° X sec⁻¹ in the frequency range of 0.25-1.7 Hz [8]. As follows from Fig. 2, the gain, maximal at subsonic frequencies, monotonically decreases with increase in the stimulation frequency.

With respect to the phase shifts between the velocity peak and the response peak, from Fig. 3 it is evident that these shifts are minimal in the subsonic frequency range, where they reach almost 50°. At frequencies of about 1 Hz the phase shift of the response relative to velocity reaches 97°. In principle it may be thought that at these frequencies the information that enters the centers from the primary afferents characterizes the coordinate to a greater degree than the velocity. If the data of Blanks and Precht [3] are considered from this point of view, then it may be considered that in their case the information going from the primary afferents of the semicircular canals of the frog at frequencies on the order of 0.5 Hz more precisely characterize the angular velocity and not the angular acceleration. The relatively larger values of the standard deviation in our case may be related not only to the functional differences of the analyzed units, but also to the impossibility of an absolutely identical contact of the wall of the canal by the vibrator rod in all the experiments. However, in principle this disadvantage in the procedure can be minimized. /54

The value of the constant τ that was calculated on the basis of the experimental data satisfactorily agrees with the value that was exhibited in the work on frogs [11]: 3 sec for a shock of constant acceleration, and it is double the value (1.9 sec) obtained with natural sinusoidal stimulation [3]. The fact that the difference in results may be due to differences in procedures is not ruled out. With sinusoidal oscillations of a rotating testing unit the cupula displacement is actively affected by both half cycles of the sinusoid: the "utriculopetal," which displaces the cupula in the direction of the utricle, and the "utriculofugal," during which it returns, passes the resting point and is displaced in the direction of the smooth portion

of the canal. In contrast to this, in the case of vibration the endolymph actively affects the cupula only during the "utriculopetal" half cycle of the sinusoid, when the microdeformation of the canal wall must cause displacement of the cupula in the direction of the utricle. Recovery of the system (as a minimum--to a position of equilibrium) occurs because of viscoelastic properties of the cupulo-endolymphatic system, as well as the mechanical properties of the membranous wall of the canal, which, according to all appearances, are frequency-dependent.

The semicircular canals and primarily the cupular apparatus itself are specialized for the transmission and transformation of low-frequency oscillations. However, it remains a fact that in the frog most of the afferents that innervate the canal clearly react to vibration with a frequency up to 100-150, and some, up to 180, Hz. Apparently this reflects the same properties of the hair cells of the vestibular portion of the labyrinth that make possible the registration of microphone potentials in response to stimulation by sound and ultrasound oscillations in the range of 0.3-100 kHz, when the microphone potentials can be observed in all the semicircular canals--the sacculus and utricle in guinea pigs [12]. It is difficult to speak of the informative significance of high-frequency responses in our case, since the phase lags of the responses here are large (to 240° relative to velocity and correspondingly to 150° relative to the coordinate of the vibrator), although in principle this does not contradict the theoretical calculations mentioned above [5]. The monosynaptic vestibulospinal connections (for example, in pigeons [1]) in some sense predetermine the possibility of the existence of vestibular input with high-speed response.

A potential applied conclusion results from the presented material: the probability of the appearance of impulsation in the neurons of the semicircular canals in response to vibration in a relatively wide frequency range. The latter is not ruled out during take-offs or during the movement of modern "extreme" means of transportation.

The employed method of direct vibration of the semicircular canal

permits investigation of vestibular responses in a wide range of frequencies (0.05-200 Hz), when the frequency overlap is 4×10^3 . In this /55 case the vibration as such does not prevent a sufficiently stable registration of the activity of the primary afferents of the vestibular nerve, including within the labyrinthine capsule, when it is not necessary to identify the afferents.

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